PREY CONCEALMENT BY AMERICAN KESTRELS

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Abstract

Experimental studies with caged American Kestrels (Falco sparcerius) indicate that the previously reported predominant dorsal orientation of cached prey may result from species-characteristic handling behavior during feeding, and that kestrels cache prey in more concealed locations when a potential food thief is present. Field observations reveal that kestrels hide prey they are feeding on when still hungry if they are about to be disturbed. These results and observations strongly support the notion that for kestrels, cache sites serve to hide as well as store uneaten prey.

Introduction

Caching behavior appears to be more widespread in owls (Collins 1976), than in diurnal raptors, where most observations are from the genus Falco (Mueller 1974). Caching is especially well documented in the American Kestrel (cf. Collopy 1977). Apparently kestrels continue to kill and cache food when satiated and cache sites act as storehouses against future uncertain prey availability, thereby insuring a more constant food supply (Stendell and Waian 1968; Balgooyen 1976; Nunn et al. 1976; Collopy 1977).

In addition to acting as storehouses, kestrel cache sites probably serve as hiding places for captured prey as both Collopy (1977) and Balgooyen (1976) noted that prey are usually cached dorsal side up in an apparent attempt to use the prey's countershading for concealment. Mueller (1974) found his captive birds reluctant to cache in the presence of either people or conspecifics. Here, I report results of laboratory experiments designed to test the hypotheses that (1) kestrels orient their cached prey to take advantage of the prey's countershading and (2) kestrels cache prey to hide it from approaching potential pirates (sensu Meinertzhagen 1959). I also report on field observations that show kestrels hide prey if they are about to be disturbed, even when apparently still hungry.

Methods and Materials

Laboratory study

I conducted aboratory experiments on 2 hand-reared, 2-year-old female kestrels and 1 wild-caught adult male kestrel. All experiments were conducted in a $1.5 \times 1.5 \times 2.0$ m cage (Fig. 1). On test days kestrels were fed 6 g of beefheart 8 h prior to testing. This assured that they were relatively hungry at the time of testing. In experiment 1, a female and the male kestrel were fed 1 mouse, either a white or black laboratory mouse (Mus musculus) or a white-footed mouse (Peromyscus leucopus). The mice were dead and were placed alternately either dorsal or ventral side up in the center of the cage floor. The orientation of the cached remains were recorded. In experiment 2 a 35 cm² opaque partition was placed halfway between corners 1 and 4 (Fig. 1). The partition visually isolated corner 1 from my observation point across the room. In this experiment the male was offered a laboratory mouse of 22–33g. After the mouse was offered, a coin toss determined whether 1 left the room to return in 45 min or whether I remained in the room tacing the kestrel while seated at a desk in plain sight 4.1 m from the cage. During observations, I remained in the room until the kestrel ap-

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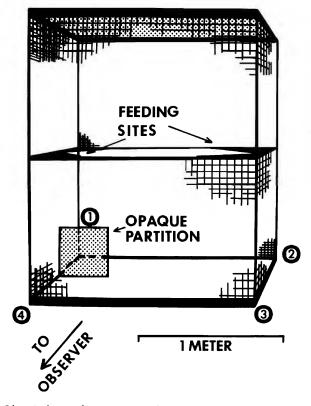


Figure 1.—Schematic of cage used in experiments 1 and 2. Circled numbers indicate corners in which kestrels cached prey.

proached, fed on, and either dropped the mouse or cached it. The location of the cached mouse and the approximate percent of mouse remaining were recorded. Prior to this experiment I practiced estimating the percent of mouse remaining from other kestrel feedings. Checks on these estimates indicated that I was able to predict within $\pm 10\%$ of the actual amount remaining 93% of the time. I later multiplied the estimated percent by the known weight of the whole mouse and subtracted that number from the whole body weight to determine grams consumed.

Field study

During the winters of 1979-81 I spent 28 h watching kestrels hunt on a salt marsh in Georgetown County, SC. Kestrels were observed at distances of from 15 to 150 m. Whenever a kestrel cached prey, I recorded species of prey, location of cache, and kestrel behavior before, during, and following caching.

Results and Discussion

Experiment 1

Experiment 1 was designed to test the hypothesis that kestrels orient their cached prey to take advantage of the prey's countershading. This hypothesis predicts that countershaded prey (e.g., white-footed mice) should be cached ventral side down while singled colored prey (e.g., white or black lab mice) should be cached with no preference for ventral side down. As the wild-caught male and hand-reared female tested did not differ significantly in this regard when caching either white (P=.50, Fisher's exact test) or black laboratory mice ($x^2=.168$, P>.50) and as they showed no difference when caching white-footed mice (Table 1), I lumped their data and tested for the effects of pelage coloration on the orientation of cached mice. Neither mouse color (black versus white mice; $x^2=.343$, P>.50) nor countershading (black and white lab mice versus white-footed mice; $x^2=.465$, P>.10) significantly altered the tendency for kestrels to cache mice ventral side down. For all types of mice both kestrels cached all individuals with the anterior end stuffed into 1 of the 4 corners of the cage (Table 1). As both birds always ate the head of the mouse first, the anterior end invariably was the end that was broken into. Sixty-four % of the mice were cached ventral side down (Table 1).

Table 1. Orientation of white and of black laboratory mice and white-footed mice cached by two kestrels in experiment 1.

Orientation of carcass			Number of mice cacheda		
side on floor	portion stuffed in corner	White lab	Black lab	White- footed	All mice
ventral	anterior	7/ 7 b	7/6	8/8	22/21
ventral	side	0/0	0/0	0/0	0/0
ventral	posterior	1/0	0/0	0/0	1/0
dorsal	anterior	1/2	2/2	1/2	4/6
dorsal	side	0/0	0/0	0/0	0/0
dorsal	posterior	0/0	1/0	0/0	1/0
lateral	anterior	1/3	1/4	2/2	4/9
lateral	side	1/0	0/0	1/0	2/0
lateral	posterior	1/0	1/0	0/0	2/0

^aThirty-six mice, twelve of each type, were presented to each of the kestrels.

In this experiment both kestrels manipulated their mice before feeding until they held the mouse ventral side down with its head extending in front of their talons. Both usually maintained this orientation throughout feeding although in several instances the prey was rotated to a side down position. After the birds flew to a corner to cache their prey

bWild caught male kestrel/captive-reared female kestrel.

they transferred it to their beak and then stuffed it into the corner. During this sequence some mice were rotated to a dorsal or side down position. In none of these instances did the kestrel reorient the mouse in the cache site.

Experiment 2

Experiment 2 was designed to test the hypothesis that kestrels cache prey to hide it from potential pirates (sensu Meinertzhagen, 1959). This hypothesis predicts that kestrels should be less likely to cache prey when a potential pirate is present and that if they do cache then they should attempt to hide the prey. Although the weights of mice offered the kestrel when I remained in the room did not differ from those offered the bird when I left (Table 2), the kestrel consumed a greater amount when I remained than when I left (33% vs. 21%; Table 2). Although I watched the bird only when I remained

Table 2. Characteristics of prey cached and the caching behavior of a wild-caught adult kestrel during experiment 2.

Experimenter	$\mathbf{p}^{\mathbf{a}}$		
•	Left room (N = 34)	Remained in room (N = 40)	
Total weight of prey			
offered (grms)	25.6 ± 3.5	26.1 ± 5.7	0.50
Amount consumed (grms)	5.5 ± 2.7	8.6 ± 5.4	0.01
Arousal calling		2.22	
(Yes/no)	0/34	9/31	0.005
Cached in corner 1b	18(53)	36(90)	0.005

aProbability of a significant difference using a t-test (weight offered and amount consumed), Fisher's Exact test (arousal calling), or Chi-square test for heterogeneity (cache site).
Pol/Percent of total cached).

in the room following feeding and thus could not compare its behavior then to behavior when I left the room, it appeared nervous while feeding in my presence, especially immediately prior to caching attempts. At those times he often moved about from perch to perch (N=38, $m=6\pm6.4$ moves) prior to caching. On 2 occasions, he retrieved cached prey and resumed eating and on 2 other occasions he flew to a cache site only to return to a perch without caching. On 9 of the 40 trials in which I remained in the room the bird gave an arousal call ("klee-klee-klee"; Cramp 1980) either prior to or during the caching sequence. Arousal calling did not occur when I left the room following feeding (Table 2). In addition to these behaviors the kestrel also shifted the typical location of cached prey in my presence (Table 2). Whereas 90% of the cached prey were placed in corner 1 when I was present, only 53% of the cached prey were so placed when I left the room following feeding. As corner 1 was the only corner available for caching that was obstructed from my view (Figure 1) this result supports the notion that kestrels cache prey in sites hidden from potential pirates.

Field study

On 2 occasions kestrels I watched from a concealed position atop a 15-m tower-blind on a South Carolina salt marsh quickly ceased feeding on their Yellow-rumped Warbler (Dendroica coronata) prey and cached the remains when an auto approached within

100–150 m. In both instances the kestrels retrieved their prey and continued feeding within 4 min following the auto's passing. Finally, I watched an adult female Northern Harrier (*Circus cyaneus*) rob a male kestrel of an unidentified passerine it was attempting to cache in a detrital rack along the salt marsh edge. The kestrel had been feeding on an exposed post along the marsh edge when it darted to the detrital rack 15 m off and began caching its prey only to be followed by the harrier.

Summary of results and general discussion

In Experiment I kestrels changed the orientation of their prey when they were feeding but not when they cached it. Based on these observations I suggest kestrel prey-handling behavior during feeding, rather than an attempt by kestrels to adjust their prey to take advantage of the prey's countershading during caching, better explains observations of kestrels caching prey ventral side down. Upon capture, falcons characteristically bite the nape or back of the skull of their prey (Cade 1960; Brown 1976). In kestrels this handling behavior results in a ventral side down orientation of small mammal prey, which appears to increase the likelihood that kestrels will cache prey ventral side down. The results of Experiment 1 also show that kestrels place their prey open end first into a cache site opening and then push the remaining body in, rather than dropping the prey in tail first. This suggests selection for concealment as the open end is often bloodied. It is possible however that this behavior was selected to prevent rapid deterioration of prey. Mueller's (1974) observations that kestrels cache intact prey more frequently than skinned prey, which would deteriorate rapidly, support this latter notion. Second, the direction of fur may make it easier for the kestrel to eat mammalian prey head first as well as to push remains into cache sites head first (Frances Hamerstrom, pers. comm.).

The results of Experiment 2 show that confined kestrels appear hesitant to cache prey in the presence of a potential pirate and that when they do cache in the presence of an intruder they increase their use of cache sites that are obstructed from view of the potential pirate. These results as well as my observations of free-ranging kestrels in South Carolina indicate that kestrels use cache sites as hiding places for uneaten prey.

For some predators cached prey is the result of surplus killing (for mammals see Kruuk 1972a; for birds see Nunn, et al. 1976), and in most instances caching behavior appears to function as a mechanism that dampens oscillations in food intake (cf. Balgooyen 1976; Collopy 1977). If caching does function to minimize fluctuations in prey availability, two criteria must be met. First, animals must be able to find the prey they have cached and second, the cached prey must be relatively safe in its cache until retrieved. Numerous studies indicate that animals, including kestrels, that cache prey are capable of retrieving stored prey (Standell and Waian 1968; Kruuk 1972a, 1972b; Mueller 1974; MacDonald 1976; Nunn, et. al. 1976; Oliphant and Thompson 1976; Collopy 1977). While most of these same investigators imply that prey is hidden from potential pirates, direct evidence is lacking. My experimental studies suggest that while dorsal orientation of cached mammalian prey may result from species characteristic prey handling during feeding, kestrels do indeed select caching sites that hide their prey from potential thieves. Additional support for a hiding function comes from field observations in Ohio (Bildstein 1978) which indicate that kestrels watch over cached prey and retrieve it when it is in apparent jeopardy. Furthermore, my observations in South Carolina demonstrate that free-ranging kestrels hide prey they are feeding on even when they are still hungry if they are approached by a potential pirate. Clearly, my experimental manipulations and natural observations strongly bolster the notion that kestrels hide and to some extent "protect" the prey they store.

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